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Original investigation

Differential predation upon sex and age classes of tuco-tucos (*Ctenomys talarum*, Rodentia: Octodontidae) by owls

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Abstract

Predation by burrowing (*Athene cunicularia*) and short-eared (*Asio flammeus*) owls upon sexes and age-classes of the subterranean herbivorous rodent *Ctenomys talarum* were studied by comparing characteristics of field-trapped and preyed-upon individuals. Owls took a greater proportion of males than females in comparison with their respective field densities. This sex-biased pattern of predation was most marked during the breeding season of *C. talarum* and mainly affected subadult males. A set of ecological features of *C. talarum*, such as food habits and above ground mobility, that might explain differential vulnerability by sex was analysed and did not support the observed pattern. We suggest that it is determined by higher above ground exposure of subadult males during the breeding season because they interact above ground with adult males and search for settlement sites to establish their own burrows.

Key words: *Ctenomys talarum*, owl predation, prey vulnerability, Argentina

Introduction

A complex set of behavioural and morphological characteristics of prey and predator species determines the likelihood that an animal will be captured. Prey activity patterns and prey habitat use are behavioural traits that may modify predation risk; while a predator's attack biomechanics, activity time or habitat use, may likewise cause certain classes of prey to be at higher risk. Non-random predation upon prey species of different size is well known among raptorial birds (Halle 1988; Marks and Marti 1984; Marti 1974; Schoener 1968; Smith and Murphy 1973; Storer 1966; Vassallo et al. 1994). Even within a single prey taxon, selection of a given size often occurs, with the young or smaller individuals often preyed upon more frequently than expected (Smith and Murphy 1973; Kotler 1985; Longland and Jenkins 1987; Donázar and Ceballos 1989; Zalewski 1996).

Predators are thought to be important factors in shaping population traits and habitat use of their mammalian prey (Kotler 1984; Jaksic 1986; Palomares and Delibes 1997; Wolff 1997; Saitoh et al. 1999). Although evidence that predation limits mammalian abundances is weak, the role of predation as a primary selective force remains undisputed in population studies. Owls and

hawks are important predators of small mammals (Marti and Hogue 1979; Korpi-mäki and Norrdahl 1989; Jaksic et al. 1992; Marti et al. 1993). Prey selection in these visually oriented predators is constrained mainly by prey vulnerability, generally an unknown function of prey size (Marti and Hogue 1979; Zamorano et al. 1984; Bozinovic and Medel 1988), prey colour (Kaufman 1974 a; Götmark et al. 1997), prey activity (Kaufman 1974 b; Longland and Price 1991), and the synergistic effects of these factors (Halle 1993). Generally, the more conspicuous sex (usually males) is more vulnerable to predators in sexually dimorphic prey (Selander 1965, 1966; Geist 1971). Moreover, even in apparently monomorphic species, body size may exhibit differences in variances between sexes, which can affect vulnerability to predation. Monomorphic species may also exhibit behavioural differences that make one sex more vulnerable than the other.

South American caviomorph rodents of the genus *Ctenomys* (locally known as tuco-tucos) are the group with most species of fossorial rodents in the world. Of about 125 living species of hypogeic rodents, 55 belong to this genus (Reig et al. 1990). Species of *Ctenomys* are sexually dimorphic, specifically male, *C. talarum* are 33% larger in body mass and 6% in body length than females (Zenuto et al. 1999).

The aim of this study is to assess the characteristics of owl predation upon sexes of *C. talarum* and to evaluate some behavioural and ecological features of *C. talarum* that might explain differential vulnerability by sex and age.

Material and methods

Four censuses of tuco-tucos, *Ctenomys talarum*, were conducted every three months starting November 1987 and throughout 1988 at Necochea (38°36′ S, 58°48′ W), Buenos Aires Province, Argentina. Each census took place in a 1.5 ha plot for five consecutive days. Each plot was staked in a grid pattern to establish the spatial location of captured animals. Animals were trapped without injury using plastic livetraps, which were placed at the entrances of all burrows and repeatedly checked and re-set until nearly all animals present within the grid were caught. Removal of individuals from census grids should have had little effect on prey availability, as total hunting area used by owls would have been much larger than the grids.

The censuses provided information on: 1) population density, 2) reproductive status, 3) body weight distribution, 4) the ratio adults: subadults, and 5) sex ratio. Fifty-nine *C. talarum* were captured, and each individual was killed by ether inhalation and autopsied to obtain information on reproductive condition, pregnancy, and relative age. Females were classified as immature (narrow, pale uterine horns and closed vagina) or mature (thick uterine horns, and open or plugged vagina). Males were also classified as immature (lack of spermatozoa in epididymis) or mature (spermatozoa in epididymis). *C. talarum* attains sexual maturity at an average weight of 95 g. Pregnant females occurred only from July to March (Malizia et al. 1991). This well-defined reproductive period in this species allowed comparisons between preyed-upon and trapped individuals during both the breeding and non-breeding seasons.

Fresh pellets from burrowing owl, *Athene cunicularia* (n = 149), and short-eared owl, *Asio flammeus* (n = 124) were collected simultaneously with our censuses. Total area for pellet collection was 10 km², which included our census grids. Pellet collection took place at known roosts, perches, or nests. Because sampling took place along consistent routes, sampling intensity did not vary among periods. Thus, number of preyed-upon individuals found in pellets should reflect predation intensity through time.

Ctenomys talarum prey remains were catalogued and then identified to species level by reference to dissected and cleaned skeletal elements of locally collected voucher specimens. The minimum number of single or double anatomical elements such as skulls, mandibles, or tooth rows estimated the minimum number of individuals in pellets. Although skulls of *C. talarum* in owl pellets were frequently found to be partially crushed, a set of skull variables could be measured. Length of maxillary toothrow, rostral width, length of diastema, mandibular length, cranial width, and basilar length were measured with a hand vernier caliper (precision 1/20 mm) and applied in the estimation of body mass and to determine sex of preyed-upon individuals. Estimation of body mass was accomplished through simple linear regression equations. Most regression equations be-

tween skull variables and body mass provided adequate models, thus allowing estimation of body mass with reasonable accuracy. Masses of prey were estimated using that variable which had the smallest sum of prediction error. Determination of sex of prey was undertaken through linear discriminant analysis (COOLEY and LOHNES 1971). Skull measurements were entered as variables for investigating within- and between group variability, testing differences in composition of groups, and finally assigning unknown prey to sex for many preyed-upon individuals. Linear discriminant as well as regression equations afforded reliable means for estimating sex and body mass of prey individuals (Tab. 1).

Additional information from a neighbour population of *C. talarum* at Mar del Cobo (37°52′ S, 57°23′ W) was analysed in order to establish presumable correlates with differential sex predation. Data from a capture-recapture study (BUSCH et al. 1989) were used to obtain information on capture frequency distributions and above ground mobility possibly related to dispersal. A second study using microhistological techniques (DEL VALLE et al. 2001) provided information on *C. talarum*'s diet characteristics. The proportion of aerial plant parts in the diet and the similarity of diet composition of an individual to that of the vegetation sourrounding each individual's burrow entrance were compared in both sexes.

Diet-vegetation similarity was expressed using the Morisita's index (LUDWIG and REYNOLDS 1988). Kolmogorov-Smirnov tests were used to compare the distribution of capture frequencies between sexes. Nonparametric Mann-Whitney U tests (ZAR 1984) were used to compare the proportion of aerial plant parts in the diet, distances moved between successive captures, and diet-vegetation

similarity indexes between sexes. Mean prey mass distributions of trapped and preyed-upon individuals were analysed with one-way ANOVA with subsequent Student-Newman-Keuls multiple comparison of means tests. Intraspecific departures from random predation were tested by calculating an expected number of individuals of each sex and age category. This was done by multiplying the proportion of each sex or age category by the total number of individuals found in pellets. Differences between observed and expected numbers of prey in pellets were tested using Chi-Square tests (SOKAL and ROHLF 1981). Alpha was initially set to 0.05 in all statistical analyses and adjusted using sequential Bonferroni corrections for the total number of comparisons in each analysis (RICE 1989).

Results

Linear discriminant analysis based on skull morphometrics produced significant separation between known males and females of *Ctenomys talarum* (Wilks' Lambda = 0.244 F = 19.783 d. f. = 5, 32 P < 0.001). We assigned skulls of *C. talarum* from owl pellets to male or female categories if the probability of correct sexual classification was ≥ 0.90. Of 112 *C. talarum* individuals found in pellets 39 skulls were intact and thus provided measurements in those variables necessary for the discriminant analysis. Regressions of body mass on skeletal measurements provided reliable estimates of body mass, allowing the assignment of

Table 1. Cranial variables and statistics of linear regressions and discriminant analysis used to estimate body mass and sex, respectively, of preyed-upon individuals of *Ctenomys talarum*. BL basilar length; CW cranial width; LD length of diastema; LMT length of maxillary toothrow; ML mandibular length; RW rostral width. Number of observations = 39.

	Body mass			Sex	
	Constant	Coefficient	r^2		
LD	−91.13	19.68	0.86	Constant	8.83
LMT	−284.48	51.83	0.67	LD	0.31
BL	−142.33	15.27	0.88	LMT	2.64
RW	−175.63	34.22	0.88	BL	0.42
ML	−179.15	17.79	0.86	RW	−3.86
				CW	−0.55
				% CORRECT	97.36

preyed upon individuals to adult and sub-adult age categories. Of the 39 *C. talarum* found in pellets we assigned 26 to males (9 adult and 17 subadult), 9 to females (7 adults and 2 subadult), and the remaining 4 were not classified (Fig. 1).

Owls showed contrasting consumption of *C. talarum*. *A. cunicularia* took most tuco-tucos during the breeding season, while *A. flammeus* preyed most heavily during the non-breeding season.

Differences in sex ratios, age category, and mean body masses of *C. talarum* were apparent between trapped and preyed-upon individuals during both breeding and non-breeding seasons (Tab. 2). Male *C. talarum* were preyed upon significantly more often than expected based on sex ratio of trapped individuals by *A. cunicularia* during the breeding season ($\chi^2 = 5.43$, P = 0.02). During the non-breeding season no individuals preyed upon by *A. cunicularia* were recorded. Sex ratio of *C. talarum* preyed upon by *A. flammeus* did not differ with respect to that expected based on trapped individuals either during this period or during the

non-breeding season ($\chi^2 = 0.73$, P = 0.39 and $\chi^2 = 1.09$, P = 0.29, respectively).

Males preyed-upon by *A. cunicularia* during the breeding season were significantly smaller than those field-trapped (SNK test, P = 0.034). The same was observed for males preyed upon by *A. flammeus* during the non-breeding season (SNK test, P = 0.017).

On the other hand, body mass of females preyed upon by *A. cunicularia* during the breeding season and by *A. flammeus* during the non-breeding season did not differ from that of field-trapped females (SNK test, P = 0.290 and P = 0.878, respectively).

That males preyed upon by owls were smaller than those field-trapped, concurs with a biased adult:subadult ratio as compared to the ratio observed in field-trapped males. Hence, subadult males were significantly overconsumed by *A. cunicularia* ($\chi^2 = 30.68$, P < 0.001) and *A. flammeus* ($\chi^2 = 53.78$, P < 0.001) during the breeding and non-breeding seasons, respectively. In both periods, the adult:subadult ratio of preyed-upon females did not show significant de-
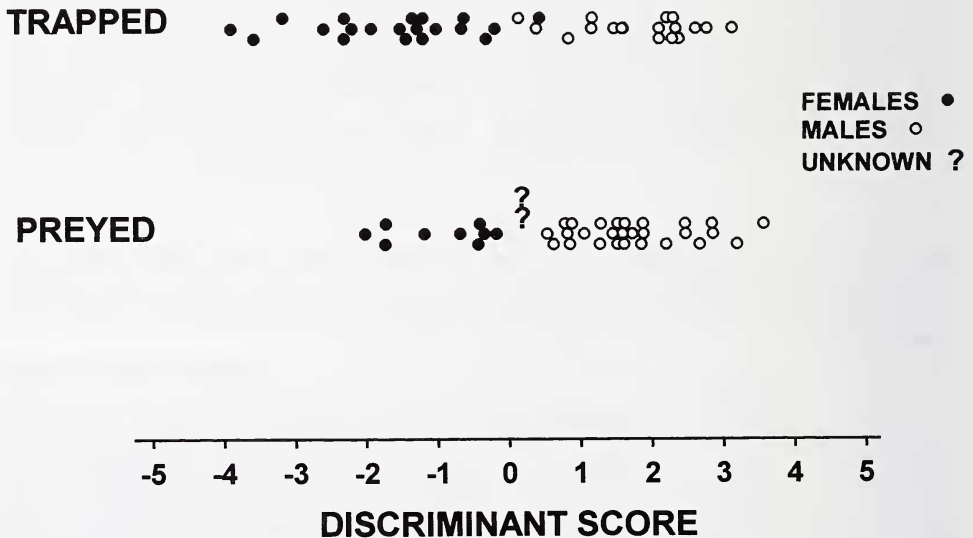

Fig. 1. Sex determination of *Ctenomys talarum* eaten by owls. Discriminant scores are given for individual craniometric measurements from known (trapped) males and females. Individuals of unknown sex in owl pellets had a probability of correct sexual classification ≥ 0.90.

partures from that observed for field-trapped individuals ($\chi^2 = 1.34$, P = 0.25 and $\chi^2 = 0.07$, P = 0.78, respectively).

The observed proportion of male *C. talarum* in both owls' pellets for the breeding season was significantly higher than that for the non-breeding season as compared to expected proportions based on field densities and sex ratios in both periods ($\chi^2 = 10.05$, P = 0.001). On the contrary, the proportion of females in owls' pellets did not differ between periods ($\chi^2 = 1.41$, P = 0.23).

A set of attributes that might indicate differential exposure to owl predation, possibly accounting for higher predation upon one sex was analysed. For this purpose we compared data on capture frequencies, distance moved between successive trappings and diet composition between sexes.

Comparisons between distributions of capture frequencies (number of individuals that were caught 1, 2, or n times) may denote differences in site fidelity between sexes, but we did not find significant differences in this regard (males 1.4 ± 0.7, females 1.6 ± 1.2; Kolmogorov-Smirnov test, D = 0.28, P = 0.92).

Distances moved between successive captures larger than the average length of the burrow system (14 m; ANTINUCHI and BUSCH 1992) were considered as above ground mobility related to dispersal, taking in account that in this species dispersal occurs above ground. Average distance for males (mean ± 1 SD, 45.36 ± 34.31 m) did not differ from that for females (43.85 ± 14.55 m; Mann-Whitney test, U = 29, P = 0.52). The proportion of these transient individuals in the population did not differ between sexes (males = 0.72, females = 0.68; $\chi^2 = 0.05$, P = 0.83).

Two attributes of the diet of *C. talarum* were presumed to be related to above ground exposure: the proportion of above ground plant parts in the diet, and the similarity between the botanical composition of the diet and that of the vegetation surrounding each individual burrow entrances. A higher proportion of above ground plant parts in the diet, and a lower similarity between diet and surrounding vegetation for one sex would indicate that this sex is more exposed to owl predation. Neither the proportion of above ground plant parts (males = 86.25 ± 12.78, females = 81.70 ± 17.61) nor diet-vegetation

Table 2. Number of male and female individuals trapped in field censuses, body mass (g; mean ± 1 SD), and observed (expected in parentheses) number of each sex and age category of *Ctenomys talarum* preyed-upon by owls.

Source of specimens and parameter	Breeding season		Non-breeding season	
	Males	Females	Males	Females
Trapped				
Total	18	23	10	8
Adults	16	16	9	2
Subadults	2	7	1	6
Body mass	129.2 ± 31.0	103.9 ± 26.5	125.4 ± 18.5	82.9 ± 20.3
Asio flammeus				
No.preyed	2 (0.9)	0 (1.1)	9 (6.7)	3 (5.3)
No. of adults	2 (1.8)	0	1 (8.1)	1 (0.7)
No. of subadults	0 (0.2)	0	8 (0.9)	2 (2.3)
Body mass	115.9 ± 0.42		83.5 ± 11.1	92.9 ± 24.8
Athene cunicularia				
No. preyed	15 (9.2)	6 (11.8)	0	0
No. of adults	6 (13.3)	6 (4.2)	0	0
No. of subadults	9 (1.7)	0 (1.8)	0	0
Body mass	88.3 ± 17.6	130.0 ± 17.0		

similarity   (males = 0.36 ± 0.18,   females = 0.36 ± 0.21)   differed   between   sexes (Mann-Whitney test, U = 337.5, P = 0.29; U = 198, P = 0.57; respectively).

Discussion

Although tuco-tucos are subterranean rodents, they occur above ground when searching for food in the vicinity of burrows, as suggested by the high proportion of aerial plant tissues found in their diet (Del Valle et al. 2001; Comparatore et al. 1995) and when dispersing (Malizia 1994). Unexpected high levels of above ground mobility have been noted in *C. talarum* (Busch et al. 1989) as well as in *C. australis* (E. Oudshoorn, pers. comm.). These above ground activities differ from what was reported for other subterranean rodent species of Spalacidae and Bathyergidae, where surface exposure is considered incidental (Heth 1991, Jarvis and Bennett 1991). The regular above ground activity of tuco-tucos would suggest that predation, principally by visually oriented raptors, is more common than previously assumed in *Ctenomys* (Vassallo et al. 1994; Busch et al. 2000). Our study shows that subadult male *Ctenomys talarum* underwent higher predation risk by owls than females during the breeding season. As a probable correlate of higher predation risk for males we compared measurements related to territory fidelity and above ground mobility between sexes and did not find significant differences. A recent experimental study concerning demographic and reproductive attributes of dispersers in *C. talarum*, at the study site of Necochea, showed a 1:1 sex ratio of dispersers, transients, and residents. In addition, dispersers did not differ from residents in age composition or body mass (Malizia et al. 1995). Thus, dispersal does not appear to be the cause of the observed predation pattern. If males and females of a prey species are equally vulnerable to predation, they should occur in owl diets in proportions approximating the sex ratio in the local environment. What characteristics of male *C. talarum* (particularly subadult males) might account for their higher vulnerabilities?

The first possibility is that subadults simply lack the experience or sensory skills necessary to avoid owl predation. Young individuals of some rodent species became prey soon after leaving maternal care due to inexperience with their new environment (Lay 1974). Young subterranean rodents leave maternal care rather late and experience the environment outside their natal nests within their mother's burrow. Size of subadult males preyed upon by owls indicate that these individuals had developed sufficient experience with their environment to be almost equally vulnerable as adult males. It is noteworthy that sizes of preyed upon males (around 85 g) clearly depart from those of natal dispersers, which are approximately 3 months old and weighed around 60 g (Malizia and Busch 1991; Malizia et al. 1991). Lower body masses of individuals captured at their exclusive burrow were around 60 g, indicating that burrow settlement occurs shortly after dispersal from their natal burrow. This suggests that preyed upon males had already established their own burrows when captured by owls.

Based on the examined information we do not have evidence to conclude that males are more vagile above ground than females. However, the possibility exists that without being more vagile, males (and particularly subadult individuals during the breeding season) stay longer above ground than females. We ask whether differential predation upon subadult males is due to coincidence of either the surface activity patterns and microhabitats used by subadult male tuco-tucos, and whether adult tuco-tucos increase the predation risk of juveniles by forcing them to stay longer above ground in more open areas.

We have no evidence concerning differences in microhabitat characteristics, i.e. differences in plant cover which eventually determine unequal exposure to visual raptors; between adult and subadult males (Comparatore 1990; Comparatore et al. 1992). However, data from semi natural enclosures concerning social and reproductive behaviour

of *C. talarum* show that adult males turn from tolerance towards young individuals to higher levels of aggression toward grown-up males (ZENUTO 1999). This observation fits with the high occurrence of scars in field-trapped males (BUSCH et al. 1989). When searching for territories – and/or a place within the social hierarchy – a considerable number of young males should be involved in aggressive interaction, which probably expose them to visually guided raptors. As opposed to females, young males near adulthood are compelled to interact and gain access to mates.

Different sources of evidence (ZENUTO et al. 1999) indicate that *C. talarum* has a polygynyc mating system in which male to male competition usually takes the form of aggressive interaction leading to dominance ranks (ZENUTO et al. 2001). Taking in account that, compared to other subterranean rodent species, *C. talarum* makes extensive use of the above ground habitat (BUSCH et al. 2000), it is conceivable that a substantial portion of social interactions – including but not restricted to inter male aggression – is performed out of their burrows. Tuco-tucos inhabit exclusive burrow systems (CONTRERAS and REIG 1965; ANTINUCHI and BUSCH 1992); only during the breeding season one of the sexes must leave its burrow and enter the other sex's burrow for mating. If males visit female burrows during the breeding season travelling above ground it is expected that males would suffer higher predation risks during this period. However, it is expected that adult males would suffer increased predation under this assumption. Some interaction between both male categories might explain higher exposure of subadult males above ground. We suggest that both the higher level of intolerance from established adult males, and the active search of a place within the social hierarchy expose subadult males near maturity to higher vulnerability to owls.

Acknowledgements

Zusammenfassung

Alters- und geschlechtsbedingte Unterschiede bei der Prädation von Tuco-Tucos (*Ctenomys talarum*, Rodentia: Octodontidae) durch Eulen

Die Prädation von Kaninchenkauz (*Athene cunicularia*) und Sumpfohreule (*Asio flammeus*) auf die Geschlechter und Altersklassen des unterirdisch lebenden, herbivoren Nagers Tuco-Tuco (*Ctenomys talarum*) wurde untersucht, indem Freilandfänge und Beutespektrum miteinander verglichen wurden. Die Eulen erbeuteten einen höheren Anteil von Männchen als nach den Dichten im Freiland zu erwarten war. Die Bevorzugung war während der Fortpflanzungsperiode von *C. talarum* besonders ausgeprägt und betraf insbesondere die Gruppe der subadulten Männchen. Verschiedene ökologische Merkmale von *C. talarum* wie Nahrungsspektrum und oberirdische Aktivität, die unterschiedliche Gefährdung der beiden Geschlechter erklären könnten, wurden analysiert, lieferten aber keine Erklärung für die Beobachtung. Wir vermuten daher, dass die vermehrte Prädation subadulter Männchen während der Fortpflanzungsperiode Folge einer vermehrten oberirdischen Aktivität ist, die durch oberirdische Interaktionen mit adulten Männchen und die oberirdische Suche nach freien Siedlungsplätzen für die Anlage eigener Baue bedingt wird.